

Speciational view of macroevolution: are micro and macroevolution decoupled?

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Abstract. –

We introduce a simple computational model that, with microscopic dynamics driven by natural selection and mutation alone, allows the description of true speciation events. A statistical analysis of the evolutionary tree so generated captures realistic features showing power laws for frequency distributions in time and size. Finally, some possible interpretations of the absence of punctuated dynamics with mass extinctions are worked out.

The novel interpretation for old paleontological observation that Gould and Eldredge [1] presented in the 70's had a deep impact on evolutionary theory. The theory of punctuated equilibrium leads not only to a change in the paradigm with which some data were analyzed, but also caused a definitive shift in the general way of thinking in theoretical biology. It has, in particular, been used as a fundamental concept to develop the idea that it is necessary to decouple micro and macro-evolutionary mechanisms.

Darwin's evolutionary theory understands the living world as the outcome of microscopic dynamics alone, driven by selection and mutation. That is, it supposes the existence of a causality in evolutionary changes driven by natural selection operating at an individual level. From this perspective, there exists a natural tendency to extrapolate such causality at all magnitudes and in time, with the hope that Darwinian natural selection alone could fully explain large-scale changes in history of life [2,3]. This traditional gradualistic approach focuses on how natural selection is capable of causing adaptation during evolution, in a process occurring at the population level that generates a continuous and progressive transformation of lineages.

In contrast, punctuated equilibrium suggests how the interposition of levels breaks this causal reduction and decouples micro from macroevolution. In this scenario, the central problem of macroevolution is to understand, through a direct study of species, which ones prevail and do better than the others, in a discrete succession of events.

A famous model of long term analysis of evolutionary processes based on the idea of a decoupled macroevolution and capable of displaying a punctuated equilibrium behavior, is the Bak-Sneppen model [4]. Here, inter-specific interactions are taken into account as the predominant force capable of generating evolution, under the simplifying assumption that the number of species is fixed and origination is prohibited.

In our approach, we will try to describe the whole mechanism of evolution by natural selection acting on individuals at a population level, in accordance with the most traditional Darwinistic view. Models with dynamics structured at the population level [5–8] or focusing on the micro-macro evolution relations [9], or also with a complex structure representing the hierarchical organization at different trophic levels [10, 11], are present in the literature.

From our point of view, they are all based on interactions that can account only for the dynamics of extinctions. Since they characterize an individual of a new species by the appearance of mutation, the processes of mutation and speciation become identified and the phenomenology of population variance within a single species is ignored. These models are thus unable to explore some problems outlined by punctuated equilibrium theory because they do not implement a dynamical mechanism that generates speciation events within a diverse population.

We will analyze instead a model where the interaction represents a natural selection responsible for speciation. Our purpose is to test if this driving force alone can account for all the phenomenology of macroevolution. For this reason, origination of new species is the crucial new phenomenon that our model must be able to account for. With this aim, we implement a self-modifying selective force based on frequency dependent selection [12, 13] that allows coexistence and branching of taxa. To sum up, we do not consider species-level fitness, but a mechanism that generates species autonomously. We do not simply perform a refilling of extinct species (as for example in Refs. [4, 5, 9, 14]) and, as a consequence, their number is not fixed. This approach also unifies the three time scales [15] that characterize evolution: the fast population dynamical scale (controlled by natural selection), the slow evolutionary scale (controlled by the mutation process) and the ultra slow macroevolution (the timescale of the speciation/extinction dialectic). Although there is no doubt that single speciation and extinction events occur by the interaction between natural selection and mutation (slow and fast scales), as stated above, there is no general agreement whether macroevolution can be seen as the simple consequence of the speciation events generated by population dynamics, without the necessity of accounting for interactions at other levels.

We will face this question by comparing the results of our model, born from this unifying view of evolution, with all the quantitative statistical properties observed in the fossil record: scale free behavior for at least some range of the distribution in time and size [16] and a time series of extinction events showing punctuated equilibrium [2] where we can find mass extinctions [17] and long term correlations [18] predominate. We will see that, although the scale free nature is reproduced, not all characteristics linked with punctuated equilibrium show up in the results.

For reasons of simplicity, the model is not developed in genotype space, as for instance in Refs. [5–7], but in the more easy-to-handle strategy space where an individual is represented by an integer number, the strategy parameter x ($0 \leq x \leq P$), that takes into account all the phenotypic characteristics that determine its biological success. At each time step, an individual generates one offspring with the same strategy as its parent, eventually mutated by a random ± 1 factor with some probability μ , that is kept constant from the start of the simulation.

We allow each agent to live until the occurrence of death caused by a selective pressure. This natural selection is characterized by two different components. The first is density-

dependent, responsible for limiting the size of the total population and controlled by the carrying capacity. The other, a frequency-dependent factor, takes into account how, in realistic situations, the tendency to occupy a more favored region in strategy space balances with an increasing competition among individuals. The latter is the dynamic component of selection, which represents the feedback between individuals and ecosystem and takes into account the instantaneous distribution of the population. Thus, natural selection is implemented through a death probability that, in the Monte Carlo simulation, takes the form:

$$S = \frac{1}{K} \cdot \sum_{y=0}^P N_y \cdot \exp\left(-\frac{(x-y)^2}{2b^2}\right) \quad (1)$$

At each time step, a random number is tossed; the individual survives if this number is larger than S . The strength of competition declines with distance in strategy space according to a Gaussian function with deviation b , and parameter K depicts the carrying capacity. x is the value of the strategy parameter of the individual that is feeling the selection pressure, and the sum runs over the y index that spans all of strategy space. By N_y we indicate the number of individuals with strategy y . We use periodic boundary conditions in order to avoid edge effects. This selective function, inspired by the ones in Refs. [12, 13], represents non-local interactions between individuals and introduces a finite wave-length instability. This selection is repulsive for individuals living in crowded regions of x -space, allowing branching and/or extinction. The mutation rate allows the conquest of new areas in strategy space and thus generates the fluctuations that can lead to the self-organization of a varying number of different strategy clusters. For this reason, it does not drive the system to an optimal ending point, but leaves it in a permanently changing dynamic state.

Since we deal with an asexual population, the biological characterization of species, defined for sexual individuals as a reproductively isolated population, must be substituted by a more operational definition, based on a functional differentiation among phenotypical distinct groups. For this reason, we refer to species as a group of individuals that share most of their phenotypic features but which differ in a few traits. According to this definition, the algorithm used associates different species to different clusters of individuals that have a small strategy distance - one being already enough - between them. That is, the space between two clusters can not be occupied by individuals. Although spatial heterogeneity or predation may have a relevant influence on the dynamics of the population and, in particular, on the frequency of branching events, they are not taken into account in our model. Additionally, a static selection component that defines the general ecological condition and can cause a directional selection, driving the population towards some fitness maximum in strategy space, does not change crucially the dynamics of the model.

The dependence of the model's behavior on the value of the parameters can be summarized by some simple rules. In general, the parameters of interest are only two, and are the ones that effectively control the branching probability. The carrying capacity (K) and the number of possible strategies (P), on the other hand, are not so crucial. In fact, the only role of the first is to regulate the population size, while P is correlated with the mean number of living species, which grows with P following a linear relation. In contrast, the mutation rate (μ) directly influences the branching probability controlling the strategy variability of the population and both the broadness of the distribution and the speed of the process. In the following we fix the value of μ so as to make possible a realistic evolutionary simulation, where mutations have to occur infrequently, which is in accordance with the fact that this parameter controls the dynamics on the slow evolutionary scale. For this reason, we set its value to 0.005. One parameter remains, b , whose value is responsible for controlling competition and, as a

consequence, the force that splits up a cluster into two different ones. This drive increases as b is decreased, causing a larger number of occurrences of branching events. There is a simple relation between the mean number of species and b , taking the form: $N(b) \propto b^{-1}$. We adjust this last parameter by searching for an equilibrium between really slow branching dynamics, which happens for large b and is a case not suitable for a statistical analysis, and small b values, for which the population feels such a strong drive that it is impossible to define an evolutionary tree. In this last situation, where the branching events are so numerous that the distribution can not be well defined, with a large number of peaks connected by intermediate strategies, it is impossible to perform a cluster analysis. An example of a realistic and living evolutionary tree generated for standard parameters values can be seen in fig. 1.

We start our analysis investigating the probability distribution of lifetimes $E(t)$ of the species, a central measure due to its comparability with observational results. From the data shown in fig. 2, we observe that a power law can be recovered

$$E(t) \propto t^{-\gamma} ; \quad \gamma = 2.02 \pm 0.04 \quad (2)$$

over about two decades, with an exponential tail for large times. These values are comparable to data from extinction records. Even if their interpretation is still under debate, it seems that a power law fitting with an exponent close to -2 is more convincing than an exponential, for at least the shorter lifetimes [16, 19]. A similar behavior was confirmed by other models as well: Refs. [5–7] agree with our value for the exponent and Refs. [9, 20] with the deviation from the power law for very long lifetimes.

The same figure shows also data related to the distribution of lifetimes for the origination processes. The life time of originations represents the time interval between one speciation event and the following one in the same lineage. These new data are of more difficult interpretation because there are no observations in the fossil records. Moreover, only models where speciation events do not coincide with extinction events (such as they do in refilling models) but are defined by an internal dynamics can produce such results. The distribution of lifetimes of originations shows also a power law behavior with $\gamma = 1.64 \pm 0.01$, with a rather extended exponential tail.

From our simulations we also obtain the distribution of extinction events as a function of their size s . By the term size we denote the number of individuals that make part of an extinct taxon from its origination until its disappearance (see fig. 3). It is possible to fit the data with a power-law: $E(s) \propto s^{-1.44 \pm 0.03}$. It is difficult to compare these results with the other ones present in the literature [5, 14] because usually the size of the events is obtained by counting the number of species or families.

From the results stated above it seems that our model is characterized by power law distributions in time and size, though restricted to some decades. However, by analyzing the distribution of lengths of intervals without activity (period of stasis), we find a clear exponential behavior (see fig. 4). If a critical process was involved, we should expect another power law. Moreover, the existence of a scale, that breaks any possible continuous connection between small, intermediate and large extinctions, is easily perceived by analyzing the time evolution of the number of extinctions (fig. 4). No mass extinctions are present and in the time series we can not recover an intermittent behavior characteristic of a punctuated equilibrium phenomenon.

Finally, we tried to detect long-range correlations in the time series of extinction events (inset of fig. 4). For correlated events, a fluctuation $F \propto t^\alpha$ with $\alpha \neq 1/2$ is expected. Moreover, the exponent α is related to the one (β) describing the power spectrum of the series through: $2\alpha = \beta + 1$. Although this result is still controversial, the study of some paleontological data [18] suggested self-similar fluctuations described by an $1/f$ spectrum ($\beta = 1$). We

analysed some time series (differing in the range of the sampling interval or in the μ value) using the DFA method [21]. No correlations were found ($\alpha = 1/2$).

Our model presents promising results showing, in accordance with observations gathered from the fossil records, a power law behavior for statistical distributions in time and size. Albeit these successful predictions, the last results show a difficulty in obtaining punctuated dynamics with mass extinctions, where long range correlations allow the clustering of the extinction events. These facts are somewhat intriguing and deserve further investigation.

It is true that the behaviour shown in our data may be an artifact of the structure of our model, which is based on an autoregulating selection that does not allow for large fluctuations in the population size. Even if this is the case, we can look at these results as a contribution to the discussion about the possibility for a unified model to represent long-term statistics of evolution.

Our model has a microdynamics of speciation based only on a natural selection force, which operates on organisms and is the exclusive responsible for adaptive evolutionary changes, in accordance with the original Darwinian paradigm [3]. We are aware that our model is just one possible implementation of such a scenario (selection based on competition) and is, in general terms, highly simplified. For these reasons it is not capable of supporting a definitive claim. Nevertheless, it is a step in the direction of stimulating the analysis in more specific frames. Some important questions are risen by our work: (a) is it sufficient to implement another more realistic and richer microevolutionary mechanism or (b) is it necessary to take into account other macroevolutionary dynamics added to natural selection [1] or, finally, (c) could it be enough to include external stresses, related with mass extinction events alone [22]?

Whatever the right answer is, we can claim to have been able to describe, through the implementation of true speciation events, the statistical distributions related to the spontaneous rate of replacement of one species by another.

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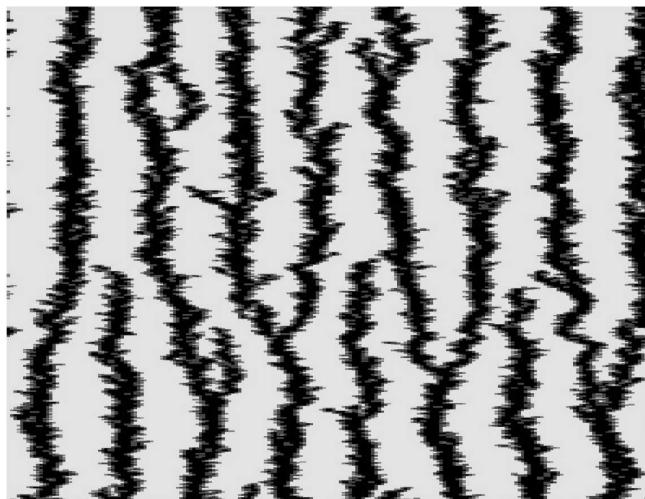


Fig. 1 – Time evolution of the population: the horizontal axis represents the strategy space ($150 < P < 300$), the vertical one the time (200000 time steps interval). The simulation ($K = 10000$, $\mu = 0.005$, $P = 500$ and $b = 15$) started with all the strategy space filled by a uniform distribution. Anyway, other initial conditions (such as, for example, a single species) generate, after a short transient, evolutionary trees that can not be distinguished from one another.

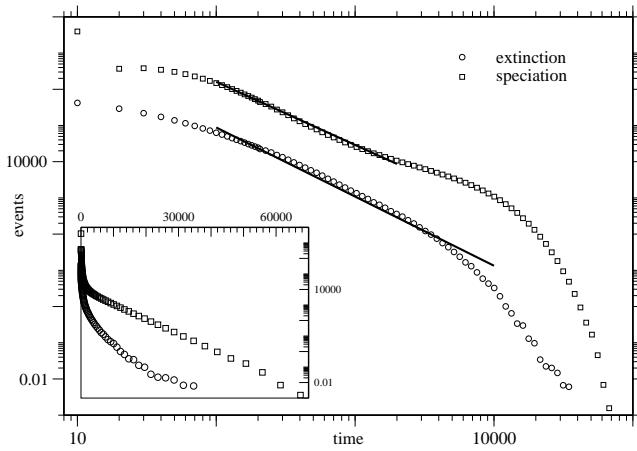


Fig. 2 – Frequency distribution for species' lifetimes. The circles represent the lifetime of extinction events (from the branching of the new taxon until its extinction), the squares the lifetime between speciation events. The inset is an evidence of the exponential tails at large times. The simulation run had the duration of 10^7 time steps and its parameters, used also in the simulations that follow, were: $K = 10000$, $\mu = 0.005$, $P = 500$ and $b = 15$.

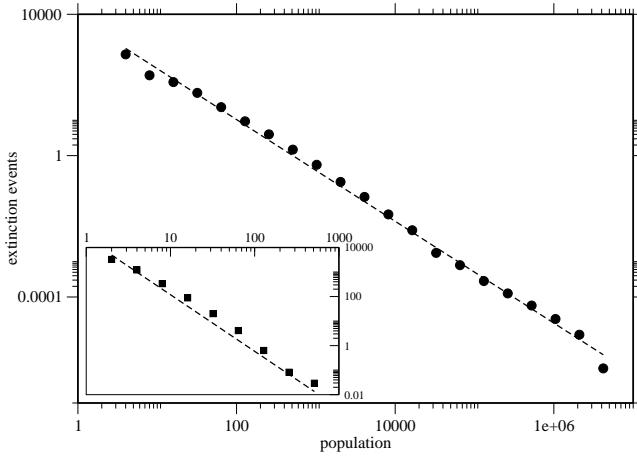


Fig. 3 – Frequency distribution for extinction size. We counted the number of all the individuals, from the branching of the new species until its extinction. The inset shows the number of individuals related to a taxon, normalized for its lifetime. In this case, the power-law takes the form: $E(s) \propto s^{-2.19 \pm 0.07}$.

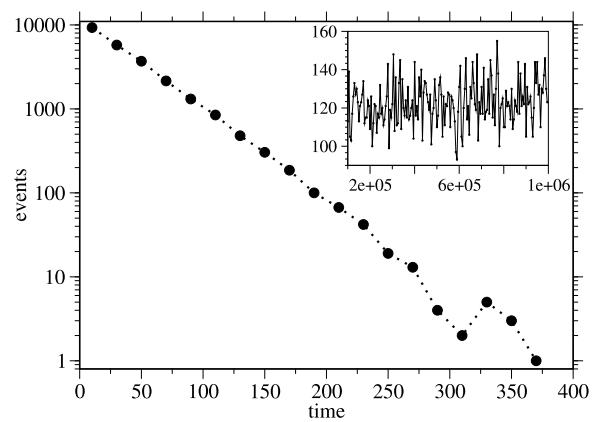


Fig. 4 – Exponential distribution of the periods of stasis. The inset shows the temporal evolution of the number of extinction events, as obtained by collecting each value in a time interval of 5000 steps.